

Temporal and Seasonal Trends in Nutrient Dynamics and Biomass Measures in Lakes Michigan and Ontario in Response to Phosphorus Control

T.H. Johengen

Cooperative Institute for Limnology and Ecosystems Research, University of Michigan, Ann Arbor, MI 48109, USA

Ora E. Johannsson

Great Lakes Laboratory for Fisheries and Aquatic Sciences, Department of Fisheries and Oceans, Burlington, ON L7R 4A6, Canada

G. Laird Pernie

NOAA/Great Lakes Environmental Research Laboratory, Ann Arbor, MI 48105, USA

and E.S. Millard

Great Lakes Laboratory for Fisheries and Aquatic Sciences, Department of Fisheries and Oceans, Burlington, ON L7R 4A6, Canada

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Results from long-term ecological monitoring studies on Lake Michigan (1983–92) and Lake Ontario (1981–92) were compared with regard to changes in phosphorus loads. In Lake Ontario, total phosphorus (TP) loads decreased from 14 000 t·yr⁻¹ in 1970 to 7500 t·yr⁻¹ in 1981, and correspondingly, midlake TP concentration decreased from 25 to 16 µg·L⁻¹. From 1981 to 1991 TP loads remained around 7500 t·yr⁻¹; however, TP concentration continued to decline from 16 to 10 µg·L⁻¹. Similarly, mean summer particulate organic carbon (POC), chlorophyll a (CHL_a), and nitrate utilization rate decreased by approximately 40, 20, and 50%, respectively. Conversely, silica utilization rates increased markedly after 1983. In Lake Michigan, TP loads also decreased by around 50% from 1974 to 1990 (2000 t·yr⁻¹); however, TP concentrations at our 100-m station in the southern basin increased during the study period from around 4 to 8 µg·L⁻¹. There were no distinct trends in CHL_a or nutrient utilization patterns; however, POC levels decreased sharply after 1987. Overall, silica utilization rates in Lake Michigan were 50% higher than in Lake Ontario (14.7 vs. 9.6 µg·L⁻¹·d⁻¹), whereas nitrate utilization rates were only half (1.4 vs. 4.1 µg·L⁻¹·d⁻¹).

Les résultats de travaux de surveillance écologique à long terme sur le lac Michigan (1983–92) ainsi que sur le lac Ontario (1981–92) ont été comparés de manière à mettre en évidence les changements dans les charges de phosphore. Dans le lac Ontario, la charge en phosphore total (PT) est passée de 14 000 t·an⁻¹ en 1970 à 7500 t·an⁻¹ en 1981; parallèlement, la concentration en PT à mi-profondeur du lac est passée de 25 à 16 µg·L⁻¹. De 1981 à 1991, la charge en PT est restée stationnaire, autour de 7500 t·an⁻¹; cependant, la concentration en PT a continué de s'abaisser pour passer de 16 à 10 µg·L⁻¹. De la même manière, la teneur moyenne estivale en carbone organique particulaire (COP) ainsi qu'en chlorophylle a (CHL_a) et le taux d'utilisation des nitrates ont diminué d'environ 40%, 20% et 50%, respectivement. À l'inverse, le taux d'utilisation du silicium s'est accru de manière prononcée après 1983. Dans le lac Michigan, la charge en PT a aussi diminué d'environ 50% entre 1974 et 1990 (2000 t·an⁻¹). Toutefois, la concentration en PT à notre station de 100 m dans le bassin sud s'est accrue durant la période d'étude pour passer de 4 à 8 µg·L⁻¹. On n'a pas décelé de tendance distincte dans la concentration en CHL_a ou dans l'utilisation des éléments nutritifs; cependant, la teneur en COP a diminué abruptement après 1987. Au bilan, le taux d'utilisation du silicium dans le lac Michigan était 50% supérieur à celui du lac Ontario (14,7 contre 9,6 µg·L⁻¹·jour⁻¹), alors que le taux d'utilisation des nitrates n'était que de moitié (1,4 contre 4,1 µg·L⁻¹·jour⁻¹).

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It has been over 20 yr since the Canadian and United States governments created the 1972 Great Lakes Water Quality Act (GLWQA) in response to accelerated eutrophication within the Great Lakes. Since that time, a great deal of effort has gone into controlling phosphorus input to the lakes, which was identified as the primary cause of the eutrophication

(Vollenweider 1968; Shapiro 1970; Schelske and Stoermer 1971). A review of earlier monitoring results (DePinto et al. 1986; Stevens and Neilson 1987) revealed that phosphorus control programs achieved significant loading reductions, and that the lakes responded to these reductions in terms of decreased phosphorus and chlorophyll concentrations.

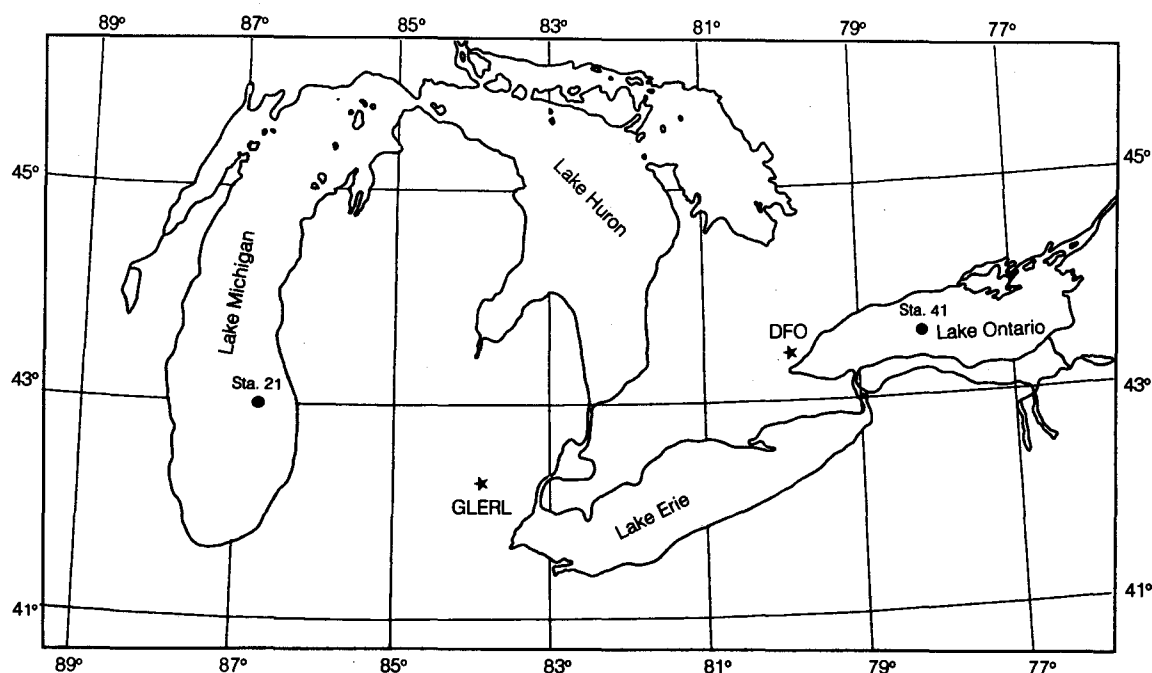


FIG. 1. Station locations for the long term ecological monitoring studies conducted by the Department of Fisheries and Oceans and the NOAA - Great Lakes Environmental Research Laboratory.

In general, however, previous monitoring studies have not been conducted with sufficient temporal intensity and duration to evaluate changes in nutrient dynamics and the response of lower trophic levels to the changes in phosphorus loadings or other natural perturbations.

We discuss the results of two long-term ecological monitoring studies conducted on Lakes Michigan and Ontario since 1983 and 1981, respectively. In both studies detailed information was collected on nutrient dynamics and planktonic community structure and abundances. These monitoring programs were developed by the Department of Fisheries and Oceans (Canada) and the Great Lakes Environmental Research Laboratory (United States) in response to the 1978 GLWQA amendments, which recognized that intensive biological monitoring was required to assess changes in the health or trophic status of lake ecosystems (Johannsson et al. 1985). The monitoring studies were designed to (1) establish detailed information on seasonal and annual trends in the physical, chemical, and biological components of the ecosystem and (2) examine the relationships and interactions among these parameters to interpret and predict changes in community structure and function. Here, we compare and contrast seasonal patterns and long-term trends in nutrient concentrations, nutrient utilization, and measures of biological activity in Lakes Ontario and Michigan, and relate these findings to changes in phosphorus loadings.

Materials and Methods

Both monitoring programs sample only a single offshore station to focus resources on temporally intensive sampling. Previous studies (Rousar 1973; Kwiatkowski 1985) have shown that sampling on temporal scales of 1–2 wk is required to adequately describe seasonal patterns in nutrient dynamics and plankton communities. In both programs, sampling occurred from approximately mid-March through November (Table 1). Details of each sampling program are discussed below.

TABLE 1. Sampling periods (days of the year) and number of cruises conducted for the long-term ecological monitoring programs on Lakes Michigan and Ontario by the Great Lakes Environmental Research Lab, Ann Arbor, Michigan, and the Department of Fisheries and Oceans, Burlington, Ontario, respectively.

Year	Sampling period		No. of cruises	
	Michigan	Ontario	Michigan	Ontario
1981		90–259		22
1982		91–278		22
1983	136–217	96–279	8	24
1984	141–236	94–289	7	24
1985	99–212	94–288	8	25
1986	86–297	100–252	11	20
1987	98–303	104–259	11	21
1988	97–306	98–280	11	21
1989	81–335	94–270	10	22
1990	90–321	93–255	15	20
1991	106–312	93–276	8	21
1992	98–337	91–282	10	22

Lake Ontario Biomonitoring Program

In the Lake Ontario biomonitoring program, sampling was conducted weekly at a midlake station (station 41) located 28 km offshore (43°43'N, 78°01'W) in approximately 130 m of water (Fig. 1). Neilson and Stevens (1986) statistically derived zones in Lake Ontario for homogeneous nutrient and chlorophyll conditions. According to their findings, conditions at station 41 are representative of the large zone of offshore water. A comparison of nutrient and plankton community structure in 1981 and 1982 at an offshore station south of Toronto with that at station 41 further supported the extent of the offshore zone (Johannsson et al. 1985).

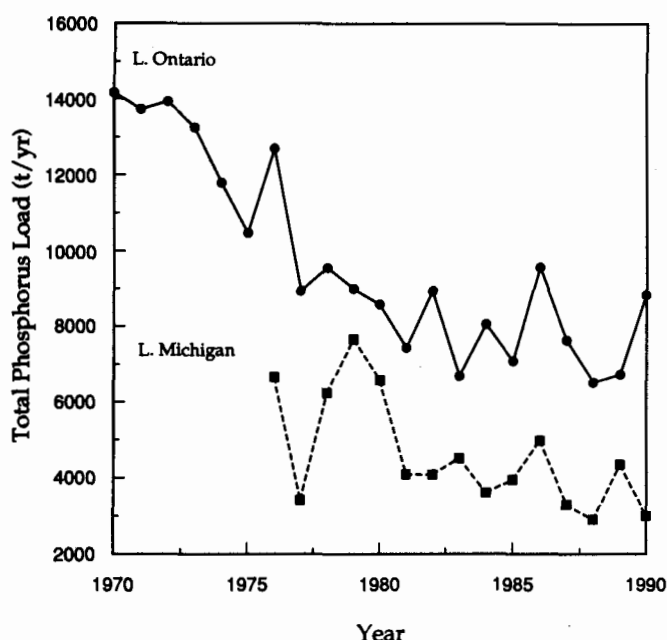


FIG. 2. Total phosphorus loads ($\text{t}\cdot\text{yr}^{-1}$) to Lakes Michigan and Ontario from 1970 to 1990 as compiled by the International Joint Commission.

Sampling protocol was determined by the thermal structure of the water column. Samples were collected from the surface to 20 m during unstratified conditions, and from surface to 1 m above the thermocline (to a maximum of 20 m) during stratification. Temperature profiles were measured by electronic bathythermograph (BT) and the mixed depth was determined by a density gradient criterion of $0.08 \text{ kg}\cdot\text{m}^{-3}\cdot\text{m}^{-1}$.

Water was collected from the specified depth range using an integrating sampler and subsampled for phytoplankton, particulate organic carbon (POC), chlorophyll *a* (uncorrected for phaeopigments) (CHL*a*), total phosphorus (TP), dissolved silica (SiO_2), and nitrate + nitrite nitrogen (NO_3).

Nutrients were determined on an autoanalyzer system using standard colorimetric procedures. TP was determined by the stannous chloride method after acid persulfate digestion of the sample. CHL*a* was determined after extraction in 90% acetone according to the method of Strickland and Parsons (1968). POC was determined on material retained on a precombusted GF/C filter using a Hewlett-Packard CHN analyzer. Phytoplankton were preserved with Lugol's solution and enumerated using the Utermohl technique. All analytical methods are described in detail in Johannsson et al. (1985). TP concentrations are reported as micrograms P per litre, NO_3 concentrations are reported as milligrams N per litre, and silica concentrations are reported as milligrams SiO_2 per litre.

Lake Michigan Monitoring Program

The ecological monitoring program for Lake Michigan was not formally established at the Great Lakes Environmental Research Laboratory until 1988; however, previous sampling efforts at the same station were conducted with enough frequency and similarity in methods that for some parameters the monitoring record could be extended back to 1983 (Table 1). SiO_2 and NO_3 were not determined

regularly during 1985 through 1987 and have been omitted for these years. Since 1988, sampling was conducted approximately biweekly from April to October at station 21, located 26 km offshore ($43^\circ 1' \text{N}$, $86^\circ 37' \text{W}$) in 100 m of water (Fig. 1).

During each cruise the water column was sampled at 8–12 discrete depths, using 5-L Niskin bottles, according to the thermal structure of the water column. Temperature profiles were determined by BT. The mixed-layer depth was defined by maximum temperature change within the thermocline. Samples were processed for the same chemical and biological parameters described above for Lake Ontario. Nutrients were determined on an autoanalyzer system using the same colorimetric procedures for NO_3 and SiO_2 . TP determinations, however, were made using the molybdate – ascorbic acid colorimetric method after the persulfate digestion. CHL*a* was determined fluorometrically on ground GF/F filters extracted in 90% acetone. POC was determined on an Oceanography International carbon analyzer after persulfate digestion. Details of the analytical procedures are given in Laird et al. (1987). To allow comparisons to Lake Ontario's integrated sample, epilimnetic concentrations were determined as the mean of samples taken from depths between 0 and 20 m ($N = 2-4$).

Data Analysis

To compare annual trends within the two lakes, data were reduced to mean values for spring and summer seasonal periods. Spring values are the means from the first sampling trip (usually late March) until the beginning of stratification. For Lake Ontario, summer values are the means of samples collected 18 d after stratification began until the mixed depth exceeded 20 m (early October). For Lake Michigan, sampling was not frequent enough to omit this transition period and summer values are the means of samples collected from the beginning of stratification through the first week of October. Correlation and regression analyses were conducted on the annual spring and summer means for each lake to evaluate relationships among measured physical, chemical, and biological parameters.

To compare seasonal patterns in nutrient and chlorophyll concentrations between the lakes, data were compiled in monthly means for the entire period of record. This procedure was used to minimize the effect of annual and climatic variability, which can greatly alter patterns in nutrient and trophic dynamics for any single year. Lastly, yearly estimates of net SiO_2 and NO_3 utilization rates were derived from linear regressions of concentration versus time. Rates were calculated for the period when concentrations decreased at the maximum rate. In Lake Michigan, the periods of maximum NO_3 and SiO_2 utilization were synchronous, whereas in Lake Ontario maximum NO_3 utilization occurred several weeks later in the season than SiO_2 . Consequently, two NO_3 utilization rates were determined for Lake Ontario. One rate represents the maximum utilization rate for the year and a second rate was calculated for the same period of time used in the SiO_2 rate determination.

Results

Annual Trends for Nutrients and Biomass Indicators

Phosphorus loading rates to both lakes were highly variable during the 1980s, but continued to show a general

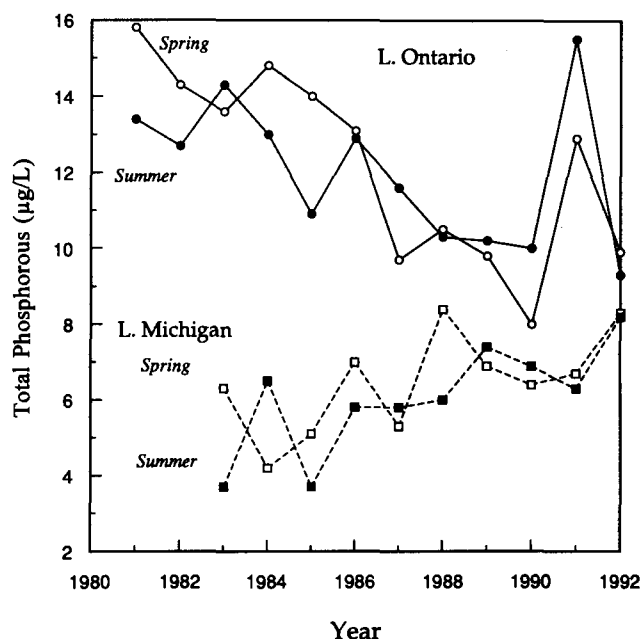


FIG. 3. Mean spring and summer total phosphorus concentrations in Lakes Michigan and Ontario for 1981–92 as determined by the Great Lakes Environmental Research Laboratory and Department of Fisheries and Oceans long term monitoring studies.

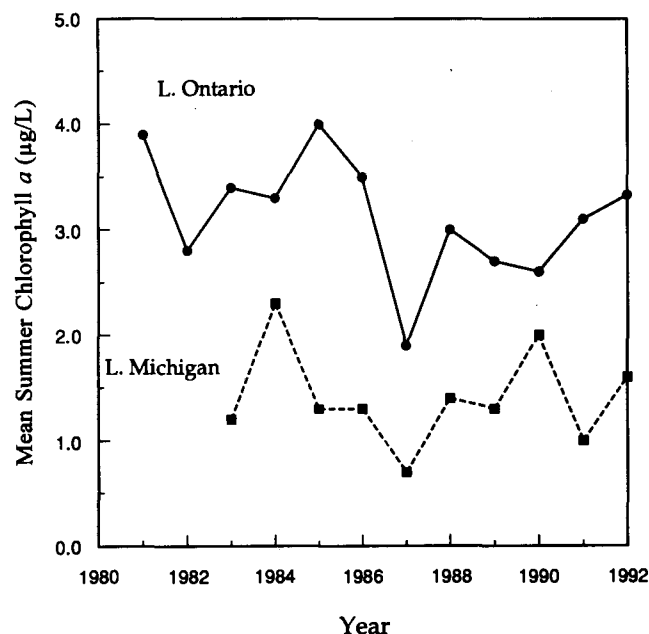


FIG. 4. Mean summer chlorophyll *a* concentrations in Lakes Michigan and Ontario for 1981–92 as determined by the Great Lakes Environmental Research Laboratory and Department of Fisheries and Oceans long term monitoring studies.

decline from previous highs in the early 1970s (Fig. 2). The load reduction in Lake Ontario ($8000 \text{ t} \cdot \text{yr}^{-1}$) was twice that in Lake Michigan ($4000 \text{ t} \cdot \text{yr}^{-1}$). Lake Ontario experienced most of the reduction in loading rates prior to 1977, whereas reductions in Lake Michigan occurred mainly after 1979.

In Lake Ontario, spring and summer TP concentrations declined during the 1980s from 14 and $16 \mu\text{g} \cdot \text{L}^{-1}$ respectively, to levels less than $10 \mu\text{g} \cdot \text{L}^{-1}$ (Fig. 3). The high TP concentration in 1991 was transitory and presumably not related to present loading rates because levels returned to the $10 \mu\text{g} \cdot \text{L}^{-1}$ range within a year. In Lake Michigan, TP concentrations were variable among years, but exhibited an increasing trend from lows of $4 \mu\text{g} \cdot \text{L}^{-1}$ in the early 1980s to highs near $8 \mu\text{g} \cdot \text{L}^{-1}$ in 1992 (Fig. 3).

Trends in CHL*a* were examined to evaluate whether changes in phosphorus levels affected phytoplankton abundance. Mean summer CHL*a* levels were variable in both lakes (Fig. 4). Summer CHL*a* levels were not correlated with spring TP concentrations in either lake or summer TP concentration in Lake Michigan; however, they were correlated with summer TP concentration in Lake Ontario (Pearson correlation, $r = 0.75$, $p < 0.01$). In Lake Ontario, summer CHL*a* ranged from 1.9 to $4.0 \mu\text{g} \cdot \text{L}^{-1}$ but exhibited an overall decline during the study period. The average level from 1987 to 1991 was 23% lower (2.7 vs. $3.5 \mu\text{g} \cdot \text{L}^{-1}$) than during 1981–1986. In Lake Michigan, summer CHL*a* varied between 0.7 and $2.3 \mu\text{g} \cdot \text{L}^{-1}$, with no apparent trend. The only similarity in CHL*a* trends was that in both lakes minimum values occurred in 1987.

POC was examined as another measure of planktonic biomass. In Lake Ontario, mean summer POC decreased by half from a high of $0.63 \text{ mg} \cdot \text{L}^{-1}$ in 1981 to $0.31 \text{ mg} \cdot \text{L}^{-1}$ in 1990 (Fig. 5). Mean summer POC was highly correlated with both mean summer TP ($r = 0.75$, $p < 0.01$) and mean summer CHL*a* concentrations ($r = 0.71$, $p = 0.01$). Lake Michigan also experienced a 50% decrease in mean summer POC

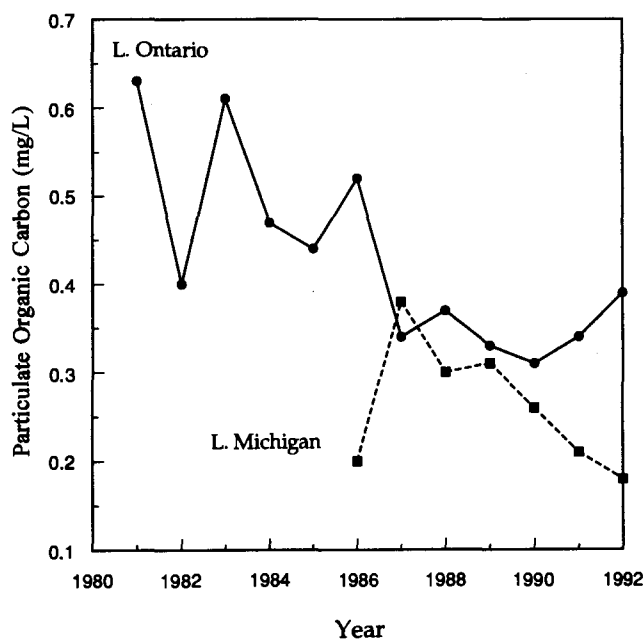


FIG. 5. Mean summer particulate organic carbon concentrations in Lakes Michigan and Ontario for 1981–92 as determined by the Great Lakes Environmental Research Laboratory and Department of Fisheries and Oceans long term monitoring studies.

during the study period. Levels declined from a high of $0.38 \text{ mg} \cdot \text{L}^{-1}$ in 1987 to a low of $0.18 \text{ mg} \cdot \text{L}^{-1}$ in 1992. In contrast to Lake Ontario, however, mean summer POC was correlated with neither TP nor CHL*a*.

Seasonal Patterns of Nutrient Use and Chlorophyll *a*

Seasonal patterns in nutrients and chlorophyll concentrations were compared to evaluate differences in phytoplankton

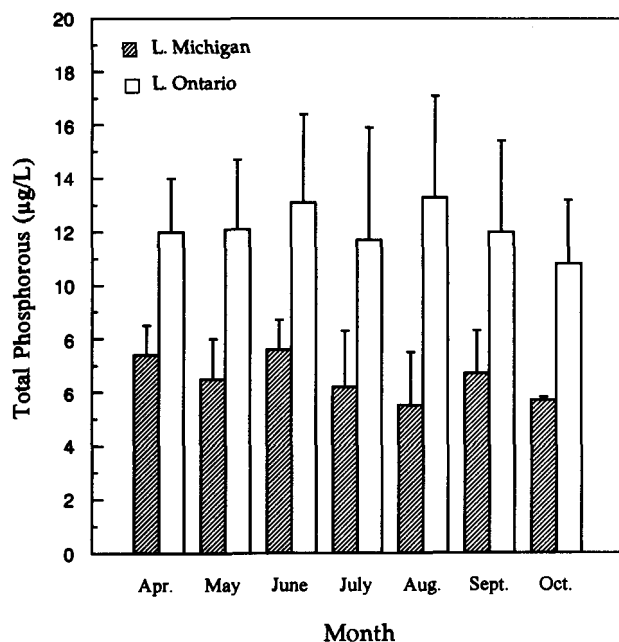


FIG. 6. Seasonal patterns for epilimnetic total phosphorus in Lakes Michigan and Ontario. Lake Ontario monthly means compiled from station 41 data collected from 1981 to 1992. Lake Michigan monthly means compiled from station 21 data collected from 1983 to 1992. Error bars = 1 SD.

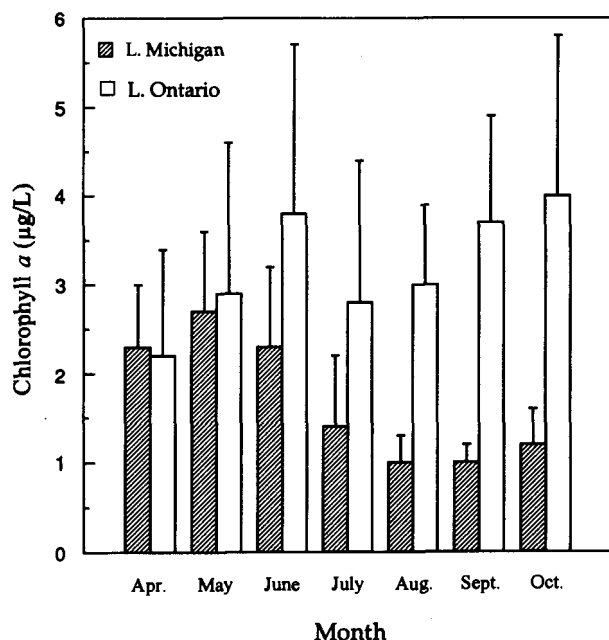


FIG. 7. Seasonal patterns for epilimnetic chlorophyll *a* in Lakes Michigan and Ontario. Data plotted as in Fig. 6.

production patterns between the two lakes. TP concentrations showed little seasonal variation in either lake from April to October (Fig. 6). The higher variability in monthly means for Lake Ontario reflects the greater change in concentration during the study. In Lake Ontario, average TP concentrations varied by $2.3 \mu\text{g} \cdot \text{L}^{-1}$ during the year, or 20% from the overall mean of $12.1 \mu\text{g} \cdot \text{L}^{-1}$. In Lake Michigan, the annual range was $1.9 \mu\text{g} \cdot \text{L}^{-1}$, or 29% from the overall mean of $6.5 \mu\text{g} \cdot \text{L}^{-1}$.

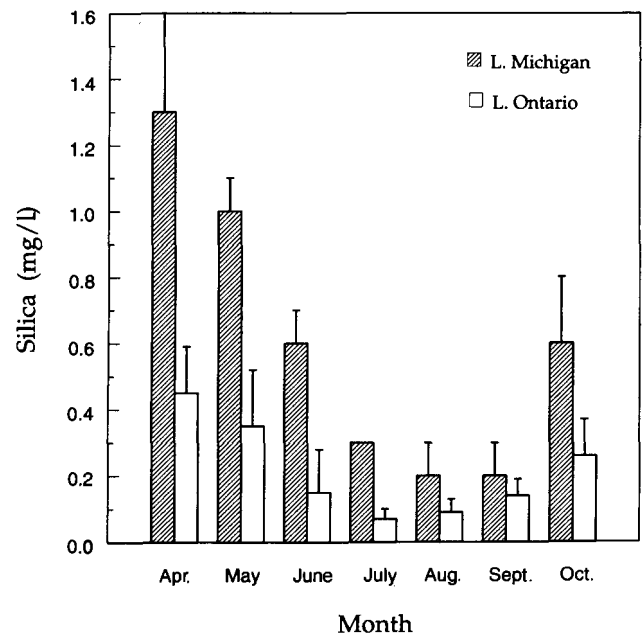


FIG. 8. Seasonal patterns for epilimnetic silica in Lakes Michigan and Ontario. Data plotted as in Fig. 6.

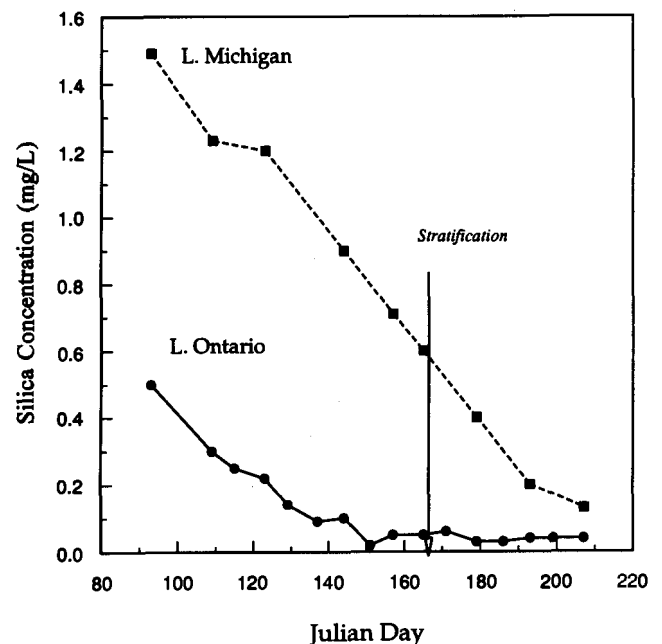


FIG. 9. A time series of 1990 epilimnetic silica concentrations in Lake Michigan (station 21) and Lake Ontario (station 41) during April to August in 1990. Typical date of stratification for both lakes is indicated.

Seasonal CHLa patterns for the two lakes reflect their different trophic status (Fig. 7). Both lakes displayed a bimodal pattern with peaks in spring and fall; however, the timing and magnitude of peaks were quite different. In both lakes, CHLa levels were approximately $2 \mu\text{g} \cdot \text{L}^{-1}$ in April and increased in May. In Lake Michigan, CHLa levels began to decline in June and minimum levels were observed from August through October. During this time, phytoplankton presumably remain phosphorus and silica limited, and are

TABLE 2. Maximum net epilimnetic nutrient depletion rates ($\mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$) for Lakes Michigan and Ontario calculated from linear regressions of concentration vs. Julian day. For Lake Ontario, a nitrate depletion rate was also calculated for the same time period used to determine silica rates. All regressions were significant ($p < 0.05$).

Year	Lake Michigan			Lake Ontario				
	Jul. day	SiO ₂	NO ₃	Jul. day	SiO ₂	NO ₃	Jul. day	NO ₃
1981				78–181	3.1	2.6	133–208	4.6
1982				152–207	6.5	4.0	152–207	4.2
1983	136–191	13.8	1.4	102–180	5.0	3.2	137–187	6.4
1984	142–187	15.6	1.4	150–177	21.8	7.8	150–177	9.3
1985				120–169	12.0	2.8	141–204	3.0
1986				119–183	9.1	2.0	133–209	3.4
1987				113–161	9.3	2.1	118–210	2.8
1988	132–195	13.2	1.3	127–168	14.5	2.0	147–182	2.9
1989	144–199	13.8	1.5	94–166	5.6	1.0	145–208	3.3
1990	141–190	16.2	1.5	93–151	7.7	0.9	115–193	2.9
1991	148–191	18.5	1.6	114–157	10.9	2.5	121–177	4.5
1992	135–204	12.0	1.4	119–162	9.4	1.2	147–240	2.4
Mean	140–194	14.7	1.4	115–172	9.6	2.7	137–200	4.1
SD		2.2	0.1		5.0	1.9		2.0

also subject to intense grazing by the *Daphnia* community (Scavia and Fahnenstiel 1987). The fall peak may be limited or delayed by the presence of actively growing phytoplankton within a deep chlorophyll layer (Fahnenstiel and Scavia 1987) that trap nutrients within the metalimnion and delay their re-entry into the epilimnion.

In Lake Ontario, CHL_a continued to increase in June and peaked at much higher levels than in Lake Michigan. Although not reflected (Fig. 7), the timing of the spring peak was much more variable in Lake Ontario and occurred anywhere from May to July for different years. The decline in CHL_a during the summer was much less severe in Lake Ontario and only lasted through August. CHL_a levels increased again in September and built to a secondary peak in October similar to that for June. The dramatic fall peak in Lake Ontario results from several factors. The deepening thermocline entrains nutrient-rich metalimnetic water, grazing pressures are reduced as temperatures drop, and there appears to be a buildup of nonedible chlorophytes (Johannsson et al. 1985). Consequently, while both lakes started out with similar CHL_a values in the spring, by fall, values in Lake Ontario are nearly four-fold greater than in Lake Michigan.

SiO₂ exhibited the most dramatic seasonal cycle of the nutrients (Fig. 8). The pattern reflects rapid utilization of dissolved SiO₂ by phytoplankton and relatively slow recycling rates after incorporation in a biogenic form. The overall seasonal patterns were similar between the two lakes; however, they differed substantially in the timing and magnitude of concentration changes (Fig. 9 and 10). Lake Michigan exhibited an SiO₂ concentration range from 1.4 $\text{mg}\cdot\text{L}^{-1}$ in the winter to a low of 0.15 $\text{mg}\cdot\text{L}^{-1}$ in August. In Lake Ontario, the concentration range was much smaller and the time needed to reach minimum levels much shorter. Concentrations were approximately 0.6 $\text{mg}\cdot\text{L}^{-1}$ in the winter and typically declined to 0.05 $\text{mg}\cdot\text{L}^{-1}$ by early July. Details of the SiO₂ utilization patterns can be seen in the concentration time series for 1990 (Fig. 9). In Lake Ontario, most of the dissolved SiO₂ pool was removed from the epilimnion prior to stratification (mean = June 15) and concentrations remained very low throughout the entire summer. During

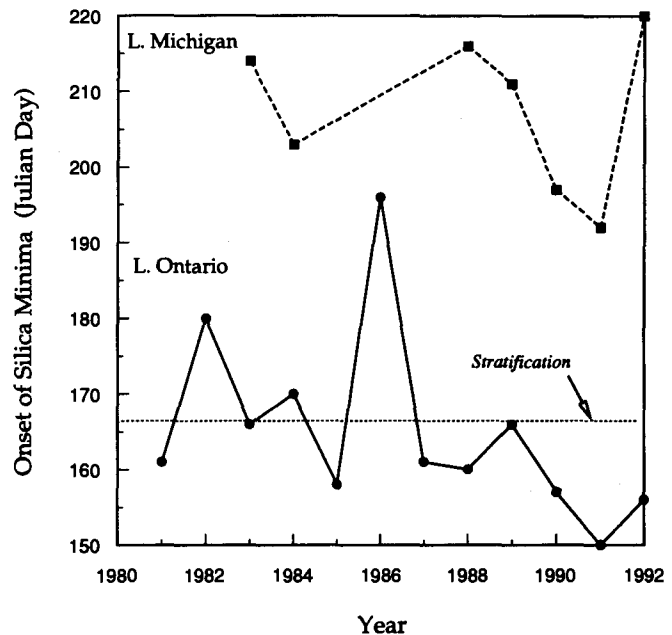


FIG. 10. Yearly estimates of the date when epilimnetic silica concentrations drop below 0.1 $\text{mg}\cdot\text{L}^{-1}$ for Lake Michigan (station 21) and Lake Ontario (station 41). Typical date of stratification for both lakes is indicated.

the study, the proportion of the dissolved SiO₂ pool removed before stratification ranged from 45 to 97%. In years when less than 70% was removed, a sharp decrease often occurred immediately after stratification. For example, in 1984 the SiO₂ concentration just prior to stratification was still 0.60 $\text{mg}\cdot\text{L}^{-1}$, but 2 wk later had fallen to only 0.07 $\text{mg}\cdot\text{L}^{-1}$. In that year, spring diatom abundance was 10% of previous levels. After stratification there was a rapid increase in diatom and chrysophyte biomass, which presumably caused the rapid decrease in SiO₂. In Lake Michigan, SiO₂ concentrations were high enough, and diatom abundance low enough, that only half of the dissolved SiO₂ pool was removed prior to stratification and minimum levels were

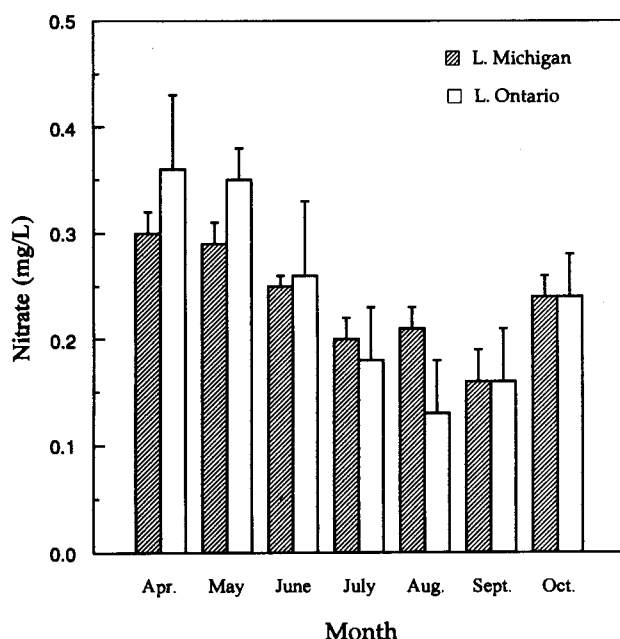


FIG. 11. Seasonal patterns for epilimnetic nitrate in Lakes Michigan and Ontario. Data plotted as in Fig. 6.

not reached until August. The proportion of the SiO_2 pool removed before stratification ranged from only 40 to 60%.

During the study period, the average SiO_2 utilization rate was 55% higher in Lake Michigan than in Lake Ontario (14.7 vs. $9.6 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$) (Table 2). Utilization rates were quite variable in Lake Ontario, however, there was a notable increase after 1983. Increased utilization rates may help explain the subsequent advancement in the onset of minimum SiO_2 concentrations for Lake Ontario (Fig. 10). Excluding 1986, concentrations dropped below $0.1 \text{ mg}\cdot\text{L}^{-1}$ progressively earlier during the year. By 1990, concentration minima were observed nearly 3 wk earlier in the year than during the early 1980s. In Lake Michigan, minimum SiO_2 concentrations occurred much later in the year than in Lake Ontario (mean day of the year = 208 vs. 165). The timing of concentration minima was quite variable among years and did not exhibit any consistent trend during the study.

NO_3 concentrations in the two lakes were much more similar than for SiO_2 and exhibited similar seasonal patterns (Fig. 11). Again, however, there were differences in the timing and rates of change between the lakes. In Lake Michigan, around 50% of the epilimnetic NO_3 was depleted throughout the year. Mean concentrations ranged from a maximum of $0.31 \text{ mg}\cdot\text{L}^{-1}$ to a minimum of $0.16 \text{ mg}\cdot\text{L}^{-1}$. In Lake Ontario, the typical annual NO_3 concentration range was slightly greater going from a winter maximum of around $0.40 \text{ mg}\cdot\text{L}^{-1}$ down to $0.12 \text{ mg}\cdot\text{L}^{-1}$.

Average NO_3 utilization rates in Lake Ontario during the study ($4.1 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$) were nearly three times those of Lake Michigan ($1.4 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$) (Table 2). In Lake Ontario, NO_3 utilization rates calculated for the period of maximum SiO_2 utilization averaged only $2.7 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$, which was still nearly double that for Lake Michigan. NO_3 utilization rates in Lake Ontario declined considerably during the study period, and rates from 1981 to 1984 were generally twice as high as those for 1985–92. Rates in Lake Michigan were very consistent throughout the study.

Discussion

Phosphorus-control programs established under the 1972 and 1978 GLWQA greatly reduced annual phosphorus loads to lakes Michigan and Ontario. The lakes are at or below the International Joint Commission's (IJC) recommended target levels of 5600 and $7000 \text{ t}\cdot\text{yr}^{-1}$ for Michigan and Ontario, respectively (Fig. 2). Loading rates may already have reached new equilibria and much of the observed variability in rates during the 1980s may have resulted from differences in nonpoint source contributions during wet versus dry years (D.M. Dolan, International Joint Commission, Windsor, ON, personal communication).

Lake Ontario demonstrated a much greater response to changes in phosphorus loading than Lake Michigan; however, the magnitude of load reduction was nearly twice as large (8000 vs. $4000 \text{ t}\cdot\text{yr}^{-1}$). This difference is even more significant given that load reductions in Lake Ontario should produce about twice the concentration change given their morphological and hydrological differences (Chapra and Sonzogni 1979). The observed loading-concentration response in Lake Ontario agreed very closely with the mathematical models that were used to set initial target loads (see Bierman 1980). Prior to 1974, spring TP concentrations in offshore waters averaged $26 \mu\text{g}\cdot\text{L}^{-1}$, but by 1980 concentrations had declined to levels around $16 \mu\text{g}\cdot\text{L}^{-1}$ (Kwiatkowski 1982; Stevens 1988). TP concentrations continued to decline throughout the 1980s and are presently below the recommended level of $10 \mu\text{g}\cdot\text{L}^{-1}$ deemed necessary to restore meso-oligotrophic conditions (Vollenweider 1968).

In Lake Ontario, the response to phosphorus control went beyond just decreased TP concentrations and was observed in changes to CHL_a and POC as well. Although changes in these variables were not strongly correlated with annual TP trends, notable decreases in both CHL_a and POC occurred between the first and last half of the 1980s. Furthermore, Kwiatkowski (1982) determined that CHL_a and POC in the offshore waters of Lake Ontario had declined by $0.8 \mu\text{g}\cdot\text{L}^{-1}$ and $0.16 \text{ mg}\cdot\text{L}^{-1}$, respectively, between 1974 and 1980. The magnitude of these changes is similar to those observed during the 1980s. It is unclear, however, why much of the observed decrease in POC and CHL_a , and shifts in nutrient utilization, appeared as stepwise changes. The abruptness of these changes suggests that factors other than phosphorus control played important roles and that effects are integrated quickly throughout the lower food web.

Unlike Lake Ontario, water-quality conditions in southeastern Lake Michigan have not responded to observed decreases in phosphorus loading. TP concentrations actually increased at station 21 over the course of the study from a low of $4.2 \mu\text{g}\cdot\text{L}^{-1}$ in 1984 to over $8 \mu\text{g}\cdot\text{L}^{-1}$ in both 1988 and 1992. This increasing trend is contradictory to earlier monitoring studies by the IJC (1989), which found no significant changes from 1983 to 1987, and to results from a time-dependent phosphorus-loading model (Lesht et al. 1991). It is difficult, however, to compare results with previous studies because of differences in sampling techniques. The IJC study was conducted at different sampling locations only three times a year, and the modeling study was conducted on data retrieved from STORET (U.S. EPA data base) without regard to temporal or spatial conditions. It is unclear whether the observed discrepancies resulted from differences in sampling techniques, or whether water-quality

trends at station 21 are not representative of conditions throughout the lake. TP concentrations did exhibit a great deal of seasonal and annual variability and, perhaps, were more influenced by exchange with coastal waters than previously believed. For example, in 1993, TP concentration increased from around $3.4 \mu\text{g}\cdot\text{L}^{-1}$ in April to $8.3 \mu\text{g}\cdot\text{L}^{-1}$ in late May after passage of the 4°C thermal front and then returned to levels around $6.0 \mu\text{g}\cdot\text{L}^{-1}$ in July (T.H. Johengen, unpublished data). TP values of $8 \mu\text{g}\cdot\text{L}^{-1}$ were commonly reported for Lake Michigan during 1979 and 1980 and the occasional occurrence of this level does not indicate that there has been deterioration in water quality. The observed TP trend at station 21 merely suggests that southeastern Lake Michigan has not responded to decreased loads.

Several factors may have contributed to the different response to phosphorus control in the two lakes. One important factor was the magnitude of load reductions in the two lakes. The total phosphorus budget model of Chapra and Sonzogni (1979), predicts that a loading reduction of 7000 t to Lake Ontario would produce a concentration reduction of $14.7 \mu\text{g}\cdot\text{L}^{-1}$, nearly identical to the observed change. For Lake Michigan, if we consider only the reduction that occurred to the main lake (i.e., minus Green Bay), loads were reduced by only 2000 t. This loading change would produce a TP reduction of $2.6 \mu\text{g}\cdot\text{L}^{-1}$. Spatial and temporal variations may be too large in Lake Michigan to detect this level of change given the present sampling techniques.

A second factor that may have affected the responsiveness of the lakes is the difference in their TP residence times. The time required for Lake Ontario to reach a new steady-state TP concentration, given a reduction in loading, is predicted to be half that for Michigan (10 vs. 20 yr) (Chapra and Sonzogni 1979). Given that the majority of load reduction to Lake Michigan occurred after 1980, it is unrealistic to expect any direct consequences at this time. In Lake Ontario, large reductions in loadings occurred from 1974 to 1980 and the present observations are well within the expected response window.

Lakes Michigan and Ontario also exhibited large differences in their patterns of nutrient utilization. These differences have developed as a result of the accelerated eutrophication of the lower Great Lakes since the 1940s (Schelske 1975). Silica concentrations have become severely depleted in Lake Ontario because phosphorus enrichment stimulated diatom production and led to increased sedimentation of SiO_2 (Schelske et al. 1986).

Net epilimnetic SiO_2 utilization rates were 55% higher on average in Lake Michigan than in Lake Ontario (Table 2). These results appear surprising, given that both diatom abundance and phosphorus concentration are much greater in Lake Ontario; however, several factors may explain the disparity. One reason utilization rates are lower in Lake Ontario (Table 2) appears to be the timing of diatom production. On average, in Lake Ontario, the period of maximum SiO_2 uptake occurred between April 28 and June 21. Consequently, most of the diatom production in Lake Ontario occurred during the prestratified period when colder water temperatures and lower light levels would slow diatom growth. Based on the difference in concentration between winter maxima (approximately $0.6 \text{ mg}\cdot\text{L}^{-1}$) and that just prior to stratification, between 45 and 97% of the epilimnetic silica pool was removed prior to stratification. In Lake Michigan, maximum SiO_2 uptake was not observed until

May 20 and typically extended to July. Based on concentration differences (assuming winter maxima of $1.4 \text{ mg}\cdot\text{L}^{-1}$), only 40–60% of the epilimnetic SiO_2 pool was utilized prior to stratification. Warmer temperatures and higher mean epilimnetic irradiance levels after stratification should promote higher rates of diatom growth and SiO_2 utilization than during the prestratified period.

A second factor that may explain lower SiO_2 utilization rates in Lake Ontario is that the average SiO_2 concentration on April 28 (the start of the period of maximum utilization) was $0.4 \text{ mg}\cdot\text{L}^{-1}$, below that considered necessary for optimum diatom growth (Parker et al. 1977). In Lake Michigan, the average concentration at the start of maximum utilization was $1.1 \text{ mg}\cdot\text{L}^{-1}$.

In both lakes, maximum SiO_2 utilization rates determined during the course of this study were higher than those calculated from earlier seasonal studies in 1969 and 1970. Calculations performed on the data of Rousar (1973) for offshore Lake Michigan indicate that in 1970 maximum SiO_2 utilization rates were around $9.2 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$, compared with the study period average of $14.7 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$. For Lake Ontario, calculations on 1969 monthly mean concentrations data (Shiomi and Chawla 1970) indicate a SiO_2 utilization rate of only $4.3 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$. This value is similar to rates observed in 1981–83, but less than half that of the study period average.

SiO_2 utilization patterns in Lake Ontario changed substantially during the study period. Maximum SiO_2 utilization rates increased sharply after 1983 and there was a marked shift in the onset of minimum silica concentrations ($<0.1 \text{ mg}\cdot\text{L}^{-1}$). Between 1981 and 1992 the onset of minimum concentrations advanced by approximately 3 wk (Fig. 11). This change was presumably caused by the increase in diatom abundance, which averaged almost threefold higher during 1987–91 than during 1981–86 (0.34 vs. $0.97 \text{ g}\cdot\text{m}^{-3}$). It is not known whether the observed changes in phosphorus levels prompted this recent change in diatom abundance.

Differences in NO_3 utilization rates between the lakes reflect their different trophic status. Maximum utilization rates averaged 2.8 times higher in Lake Ontario than in Lake Michigan. This difference is expected given higher phytoplankton abundances and phosphorus levels in Lake Ontario. NO_3 utilization rates appear to have responded to changes in phosphorus levels within Lake Ontario. NO_3 utilization rates exhibited a decreasing trend throughout the present study period as phosphorus levels continued to decline. However, data from Shiomi and Chawla (1970) indicate that maximum utilization rates in 1969 were around $2.2 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$, or nearly half the 1980's average.

In Lake Michigan, NO_3 utilization rates did not change during the study period, even though there was an apparent increase in TP concentration. Based on the data of Rousar (1973), present day NO_3 utilization rates agree closely with those found in 1970.

Conclusions

Long-term ecological monitoring studies, conducted on time scales of weeks, are required to adequately describe both seasonal and annual changes in nutrient and lower food-web trophic dynamics. Lower trophic levels in Lake Ontario have responded to phosphorus control programs. Changes in phosphorus concentration agree well with those predicted

by models used to set recommended target loads. During the past decade there have been changes in POC, CHL_a, and nutrient utilization rates, which would suggest that Lake Ontario appears to be shifting towards more meso-oligotrophic conditions.

Southeastern Lake Michigan has not responded to reduced phosphorus loads. The lack of response may in part be due to the magnitude of loading change and the time required to reach a new equilibrium concentration. Additionally, large seasonal and annual variability at the present monitoring station may be masking trends in other parts of the lake.

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